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A trait database for Guianan rain forest trees permits intra- and inter-specific contrasts

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Abstract – We present a plant trait database covering autecology for rain forest trees of French Guiana. The database comprises more than thirty traits including autecology (e.g., habitat associations and reproductive phenology), wood structure (e.g., density and tension characteristics) and physiology at the whole plant (e.g., carbon and nitrogen isotopes) and leaf level (e.g., specific leaf area, photosynthetic capacity). The current database describes traits for about nine hundred species from three hundred genera in one hundred families. For more than sixty species, data on twelve morphological and ecophysiological traits are provided for individual plants under different environmental conditions and at different ontogenetic stages. The database is thus unique in permitting intraspecific analyses, such as the effects of ontogenetic stages or environmental conditions on trait values and their relationships.

plant traits / tropical forest / French Guiana / functional groups / plasticity / ontogeny

Résumé – Une base de données sur l'autécologie des arbres de la forêt tropicale de Guyane française. Nous présentons une base de données sur l'autécologie des arbres de la forêt tropicale de Guyane française. La base contient des données sur plus de trente traits concernant l'autécologie (par exemple, les préférences d'habitat et la phénologie reproductive), la structure du bois (par exemple, la densité et les caractéristiques du bois de tension) et la physiologie aux niveaux de la plante entière (par exemple, les isotopes du carbone et de l'azote) et de la feuille (par exemple, la surface spécifique ou la capacité photosynthétique). Dans son état actuel, la base décrit les traits d'environ neuf cents espèces de trois cents genres dans cent familles. Pour plus de soixante espèces, des données sur douze traits morphologiques et écophysologiques sont fournis au niveau individuel pour des plants dans différentes conditions environnementales à différents stades ontogéniques. Cette base de données permet donc des analyses intraspécifiques, comme les effets des stades ontogéniques ou des conditions environnementales sur les valeurs des traits et leurs relations, ce en quoi elle n'a pas d'équivalent.

traits / forêt tropicale / Guyane française / groupes fonctionnels / plasticité / ontogénie

1. INTRODUCTION

Databases compiling species traits are important tools for plant ecologists to understand patterns of species abundance and distribution at a time of rapid loss of species diversity [10, 16, 17, 23, 24]. Recent studies have underlined at least four compelling research applications for such databases. First, trait databases can help us to understand basic strategies of resource use or biomass allocation among plants. Recent compilations [10, 34, 51, 52] illustrate how data from many different sources can be combined to confirm general conclusions of plant functioning that have been suggested from local datasets. Second, trait databases permit comparisons and contrasts of species diversity and plant functional types across natural environmental gradients, both within and among systems. For example, several studies demonstrate how trait values such as high foliar nutrient content are associated with particular environmental conditions such as high annual precipitation [33, 49, 50]. Third, trait databases are being used to select focal species for experimental communities to test relationships between species diversity, functional diversity and

ecosystem function [21, 40], or to refine subsequent analyses for existing experiments [31]. More recently, a fourth objective has been underlined, to understand evolutionary patterns among trait associations, such as the origin of seed mass associations with other plant traits [27, 28].

In general, within-species analyses for continuous traits, such as leaf attributes, use a mean trait value for species, without consideration of the variability masked by that mean value. To address this gap, we propose a fifth application of trait databases of a particular construction, within-species analyses. We recognize three particular types of intra-specific variability that could influence the mean value of traits reported in most databases, noting that analyses of each of these levels of variation represent advances for the application of trait databases. First, the observed phenotype of many plant traits can be strongly influenced by genotype of individuals for which trait screening has been conducted; we refer to this as the effect of *genetic diversity*. For example, Balaguer et al. [1] found significant differences in biomass allocation patterns and foliar nutrient contents among *Quercus coccifera* seedlings from three Mediterranean ecotypes differing in isozyme patterns. A second level of intraspecific trait variability occurs based on

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the environmental conditions under which measurements are made; we refer to this as *species plasticity*. For example, foliar traits are often reported for ‘sun leaves’, but the definition of sun may include plants grown in pots under high transmission shade cloth and those in the field under open conditions [48]. In some cases, these environmental effects can interact with genotype effects so that the observed phenotype is the result of genotype \times environment interactions; for example, in the study by Balaguer et al. [1], the three ecotype populations responded differently when grown in sun vs. shade. A third level of variation that may occur within species involves differences in trait values with plant size or developmental stage; we refer to this as *ontogenetic plasticity*. In a recent meta-analysis, for example, Thomas and Winner [47] report significant differences between saplings and adult trees of 35 tree species, for several photosynthetic traits.

In this paper, we present MARIWENN, a trait database for woody plant species of the Guiana Shield region of South America that has been constructed to permit both intra- and inter-specific contrasts. First, we describe the construction of the database and the sources of available data; in doing so, we contrast the design and potential uses of the database with those of other plant trait databases such as GLOPNET and LEDA. We then present some examples of analyses that can be conducted using the database, including the unique aspect of within species comparisons in addition to the contemporary interspecific contrasts.

2. CONTENT

We gathered plant trait data for more than nine hundred woody plant species from French Guiana, representing over three hundred genera in more than one hundred families. Many data sources appear only in the grey literature, and thus would not otherwise be easily accessible to all researchers. The first part of the database was built to be an exhaustive compilation of the results of research on general species traits. No standardization of the data was made at this step; the purpose was just to organize the data rigorously to allow users to find data sources and the methods employed. The result is a comprehensive synthesis of data covering fields from wood structure to reproductive phenology (Tab. I). The modular structure of the database allows new data to be entered as it is generated.

The second purpose of the database was to structure data of plant traits to allow multivariate analyses. Unlike the first approach, this framework requires normative rules of measure and organization of the data. Moreover, specific measures are required to structure the database. The trait list reflects the state of the art of research and may change according to demands and new discoveries (Tab. II). Unlike the GLOPNET [23] databases, MARIWENN contains trait values measured on individual plants. Each value is then linked to many other fields that permit more complex queries: details of measurements (protocol); its author (reference); the environment, described with two levels of detail (general environment such as glasshouse or canopy, and detailed environment indicating the soil or the topographic position, or light level); and the ontogenetic stage of the plant. The mean and standard deviation of the trait can be computed as requests are made, for each ontogenetic stage and each environment type. Filters are available to reduce the dataset to a chosen light

level or detailed environment. This organization allows the retention of a large number of individuals or the isolation of particular environmental conditions, as a trade-off between sample size and variability among individuals.

The recorded traits are based on those described by Cornelissen et al. [7], without limitation (Tab. II). A priority of recent research has been leaf traits, including: specific leaf area, leaf area, laminar thickness, foliar carbon, nitrogen and phosphorus contents, and photosynthetic traits. An intensive campaign of measurement is being processed to enhance the database.

The botanical database is a straight adaptation of the checklist of the plants of the Guianas [3], including, where possible, a reference to the herbarium of Cayenne (IRD). Taxonomy is detailed down to the variety or subspecies, even though the standard level of detail is the species. Vernacular names are available as supplementary information. However, we caution the use of the database as a source of cross-referencing between scientific and common names because these links often vary between regions. The sites of field and experimental studies are referenced and their main characteristics detailed for each entry.

We chose to develop the database to maximize its versatility. No data related to the studied species are excluded a priori. The geographic limit is that of the botanical database which includes the plateau of the Guianas. The present content of the database is restricted to forest trees, but data from mangroves, savannas or non ligneous vegetation will be added as future research programs provide them.

3. USING THE DATABASE

All the published data are available through the Internet on <http://ecofog.cirad.fr/Mariwenn>. Unpublished data may be available in advance upon request of a password from the corresponding author. Future work will naturally be keeping data compilation up to date and also completing the trait records at plant level. We hope to gather individual data for most of the traits of the 100 most abundant woody species in French Guiana within two years.

Data can be obtained by species (all data available for a given species) or by topic (all species available for a given subject).

The web access is particularly easy to use but does not allow complex queries. Direct access using SQL queries is possible from the local network only, for technical and security reasons. Scientific collaborations are thus the easiest way to obtain complete access to the database, and interested researchers are invited to contact the corresponding author.

3.1. Examples of intraspecific analyses

In its current state, the database allows analyses within species for variation between environmental conditions, or between ontogenetic stages (see examples suggested in Tab. III). Current collections for trait screening are following half-sibling cohorts within species and will thus permit contrasts to be made to analyze ‘genotype’ or genotype \times environment effects on trait values.

Table I. Traits that have been measured at the species level that can be used in interspecific comparisons within this database or in concert with other databases, across sites or biomes.

Trait	References
<i>Ecophysiological data</i>	
Nitrogen: Isotopic signature ($\delta^{15}\text{N}$) and leaf nitrogen concentration in various forest sites	[35–38]
Carbon: $\delta^{13}\text{C}$ values and leaf carbon concentration at several sites	[4]
Photosynthesis-related ecophysiological parameters measured in glasshouse	[8]
<i>Biomechanics</i>	
Wood density at 12% moisture	[5]
Wood durability, impregnability; durability against termites and fungi	[14, 15]
Tension wood characteristics	[41]
<i>Soil-vegetation relations</i>	
Characterization of the edaphic preferences of species	[6, 30, 45]
<i>Architecture and phenology</i>	
Seedling morphology	[2]
Architectural patterns of trees	[18–20]
Vegetative phenology	[26]
Reproductive phenology	[9, 26, 42–44]
<i>Reproduction</i>	
Seeds and fruit characteristics	[2, 6, 12, 26, 42]
Pollen dispersal	[9]
<i>Forest dynamics</i>	
Pioneer species and soil seed bank	[29]
Response groups of species for light	[11]
Height groups: position of species in the vertical structure of the forest	[6]
Horizontal spatial structure of tree species	[6]

Table II. Traits describing species morphology and physiology that have been measured for individual plants for a given ontogenetic stage and under particular controlled environmental conditions, thereby permitting intra-specific analyses of species' plasticity across different environmental gradients, or ontogenetic shifts in trait values.

Trait	Unit	Measurement
Relative growth rate (RGR)	$\text{mg g}^{-1} \text{d}^{-1}$	After Hunt [22]
Root-shoot ratio	g g^{-1}	Root biomass/shoot biomass
Specific leaf area	$\text{cm}^2 \text{g}^{-1}$	leaf area/leaf biomass
Leaf blade surface area	cm^2	LICOR 3000 meter
SPAD chlorophyll estimation	SPAD units	Minolta SPAD-502 meter
Leaf thickness	μm	Mitutoyo caliper
Leaf dry matter content	mg g^{-1}	After Garnier et al. [13]
Leaf mass ratio	g g^{-1}	Leaf area/total biomass
Net assimilation rate (A_{max})	$\mu\text{mol CO}_2 \text{cm}^{-2} \text{s}^{-1}$	CIRAS-1 System
Dark respiration rate (Rd)	$\mu\text{mol CO}_2 \text{cm}^{-2} \text{s}^{-1}$	CIRAS-1 System
Stomatal conductance (Gs)	$\mu\text{mol CO}_2 \text{cm}^{-2} \text{s}^{-1}$	CIRAS-1 System
Foliar [d13C]	‰	Mass spectrometer [4]
Foliar [N]	‰	CHN autoanalyzer
Foliar [P]	‰	HF digest; colorimetry
Water use efficiency (WUE)	$\mu\text{mol H}_2\text{O mol}^{-1} \text{CO}_2$	A_{max}/Gs
Nitrogen efficiency index (NUE)	$\mu\text{g g}^{-1} \text{d}^{-1}$	Foliar [N]/RGR
Phosphorus efficiency index (PUE)	$\mu\text{g g}^{-1} \text{d}^{-1}$	Foliar [P]/RGR

Table III. Examples of intra-specific calculations of species' plasticity or performance response ratios, across different environmental gradients, that can be performed using the MARIWENN database.

Calculated index	Unit	Calculation
Response ratio - Light	%	$RGR_{\text{hilight}}/RGR_{\text{lo light}}$
Response ratio - Soil moisture	%	$RGR_{\text{hiSM}}/RGR_{\text{loSM}}$
Response ratio - Soil nutrients	%	$RGR_{\text{hiSN}}/RGR_{\text{loSN}}$
Plasticity in SLA	%	range of SLA/SLA_{max}
Plasticity in WUE	%	range of WUE/WUE_{max}
Plasticity in NUE	%	range of NUE/NUE_{max}
Plasticity in root-shoot allocation	$g\ g^{-1}$	range of RS/RS_{max}
Plasticity in leaf area ratio	$cm^2\ g^{-1}$	range of LAR/LAR_{max}

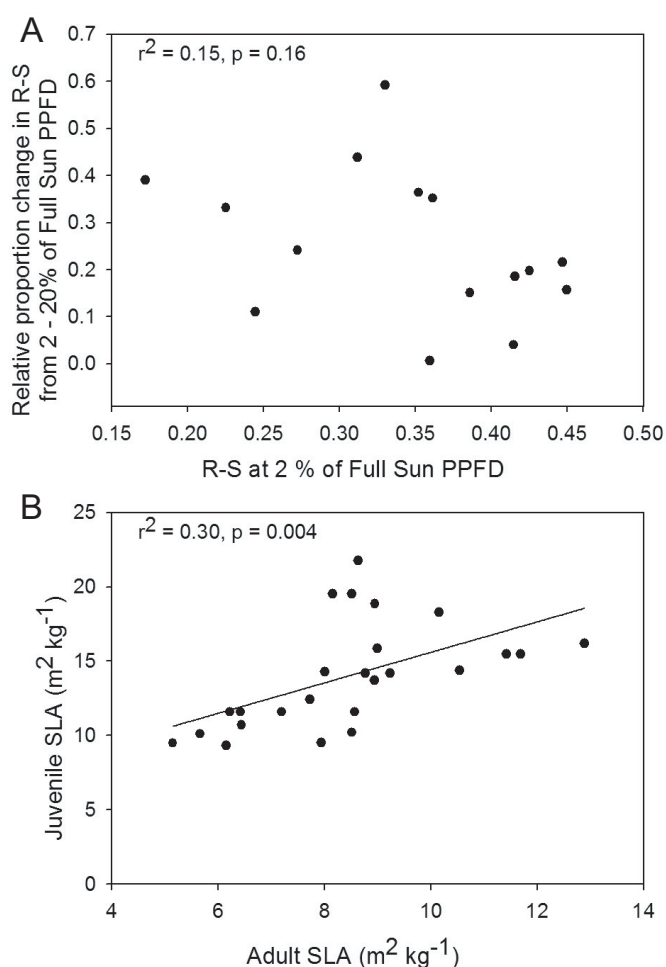


Figure 1. Examples of intra-specific analyses that can be conducted using the MARIWENN database. (A) Do species with particular mean values of a given trait exhibit greater breadth in trait values across a range of environmental conditions? In this example, we test whether species with low root-shoot ratio (R-S) have a larger range in R-S (relativized to maximum value; see Tab. II), across a light gradient varying from 2–20% of full sun. Data from C. Baraloto, unpublished. (B) Do species maintain trait values throughout developmental stages and/or size classes? In this example, we test whether mean values for SLA of sun leaves for 25 species change between juveniles and adult trees. Data from C. Baraloto and D. Bonal, unpublished.

Figure 1 illustrates two types of analyses that can be conducted using queries of the current database. The first example examines, for a given ontogenetic stage, if species-level trait breadth differs among species. In this case, the example addresses a species-level scenario for the hypothesis of Taylor and Aarssen [46] or Lortie and Aarssen [25] who suggest that a greater breadth of traits related to fitness should be exhibited by generalist species because they are exposed to selection under heterogeneous environments. If it is assumed that among tropical tree seedlings, the more specialized ecological guild is the light-demanding species, who generally have low root-shoot ratios [32], then we would predict a negative relationship between trait breadth and trait value in this case. However, no significant relationship was found for the species in the MARIWENN database (Fig. 1A).

The second example tests whether trait values, at a given environmental level (in this case leaves exposed to full sun) differ between developmental stages. Figure 1B shows a significant relationship between adult and juvenile specific leaf area (SLA). Nonetheless, a large degree of variation exists around this relationship, and many species pairs switch relative positions between stages. Moreover, as with the study of Thomas and Winner [47] or that of Roggy et al. [39], adult leaves have consistently lower SLA (or higher LMA).

3.2. Using these results to refine interspecific analyses

Each of the above examples shows how the intra-specific analyses can respond to particular research questions. In addition, we suggest that these types of analyses should serve as precursors to species-level analyses. When we find significant effects of environment or stage on mean trait values, this suggests that these factors need to be considered when conducting analyses among species. In the first example, (Fig. 1A), it is clear that the magnitude of shifts in root-shoot ratio between light environments differs among species (although not predictably based on a given trait value). This suggests that the results of multivariate analyses among species would be strongly dependent on the environmental conditions under which plants were grown for trait screening. Such variation may occur at what we have called the detailed environment, as in our example, or at what we have called the general environment.

For example, growing species in pots may influence the values of traits such as specific root length or root-shoot ratio (K. Kitajima, pers. comm.). The second example (Fig. 1B) indicates that for the 25 tropical tree species, multivariate analyses of foliar trait associations including specific leaf area (SLA, or its inverse, LMA), such as those conducted by Wright et al. [52], should control for the developmental stage of the plants measured in the database because species' values may shift rankings between stages.

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